

Palatal Thickening and Facial Form in *Paranthropus*: Examination of Alternative Developmental Models

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KEY WORDS extant hominoids; fossil hominids; sutural mechanics; subnasal morphology; posterior facial hyperplasia

ABSTRACT *Paranthropus* is distinctive among hominoids in its possession of a greatly thickened hard palate. Although traditionally considered a structural adaptation to counter high-magnitude masticatory stress, alternative developmental models are equally viable. Three models of palatal thickening were evaluated in this study. A mechanical model interprets palatal thickening as a compensatory response to increased instability of the midpalatal suture effected by an anterior placement of the masseteric muscle mass. This model predicts that palatal thickness is correlated with the length of the palate posterior to the masseteric tubercle. Two non-mechanical models consider the thickness of the hard palate to be structurally related to and therefore correlated with either 1) the degree to which the premaxilla overlaps the hard palate in the subnasal region or 2) the height of the posterior facial skeleton. The correlation of craniofacial variables was assessed intraspecifically in ontogenetic series of great ape and human crania. Tests of correlation were performed for each comparison using both residuals calculated from reduced major axis regression of the variable of interest against a measure of cranial size and shape ratios. A significant correlation of palatal thickness with posterior facial height in *Pan* suggests that the unusually thick hard palate of *Paranthropus* is directly related to the increased posterior facial height characteristic of this taxon. Further evaluation suggests that extreme palatal thickening in these specimens occurred by virtue of their possession of a nasal septum morphology in which the vomer extends onto the superior nasal surface of the premaxilla. Such a morphology would have constrained the palatal nasal lamina to maintain the approximate level of the premaxillary nasal lamina throughout the growth process thereby promoting palatal thickening. Am J Phys Anthropol 103:375-392, 1997.

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Analysis of the phylogenetic and ecological relationships of the early hominids is dependent upon a clear understanding of the developmental basis of craniofacial variation observed in this sample. Although the unusual dental and cranial adaptations of the robust australopithecines have attracted the attention of paleoanthropologists for many years, the facial morphology of these specimens has only recently begun to be

scrutinized in detail with respect to alternative models of growth and development (McCollum, 1994). *Paranthropus* is distinctive

Contract grant sponsor: Sigma Xi; contract grant sponsor: Boise Fund.

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Received 31 July 1995; revised 18 February 1997; accepted 20 March 1997.

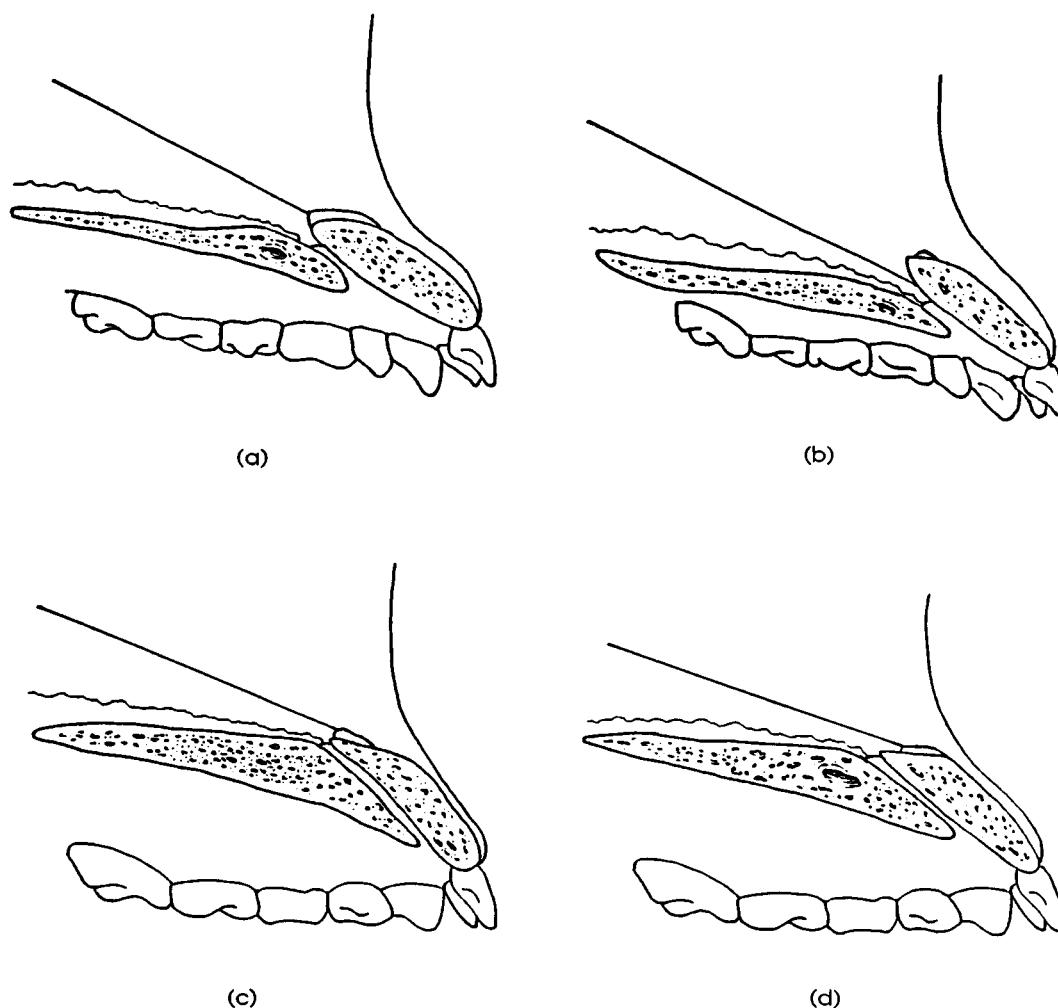


Fig. 1. Schematic sagittal sections of the subnasal morphologies of (a) *A. afarensis*, (b) *A. africanus*, (c) *P. robustus*, and (d) *P. boisei*. Note the thick palates typical of robust australopithecine taxa.

among hominoids in its possession of a greatly thickened anterior hard palate (i.e., paired palatal processes of the maxillae; Fig. 1). Results of a previous evaluation of *Paranthropus* facial form (McCollum, 1994) suggested that the unusually thick hard palate characteristic of this taxon potentially played a significant role in the development of numerous other facial features that distinguish these specimens from other early hominid taxa. The present analysis evaluates alternative developmental models of palatal thickening in *Paranthropus*. The models considered encompass both mechanical explanations, which have dominated the thinking of researchers ever since Robinson (1953,

1954) first identified this unusual morphology (e.g., Rak, 1983), and alternative non-mechanical models that have emerged from recent analyses of extant hominoid and fossil hominid subnasal morphological variation (McCollum et al., 1993; McCollum and Ward, 1997) and early hominid facial ontogeny (Bromage, 1989, 1992).

MODELS OF PALATAL THICKENING IN *PARANTHROPUS*

Sutural reinforcement

In his comprehensive evaluation of australopithecine facial morphology Rak (1983) suggested that the unusually thick anterior

hard palate characteristic of the robust forms served to reinforce the sutural interface between the two halves of the dental arcade during unilateral biting. Assuming that the maxillary zygomatic process functions to support (e.g., "buttress") the posterior aspect of the hard palate during contraction of the medial pterygoid muscle, it was argued that the anterior placement of the maxillary zygomatic process (Rak's lateral buttress) in the facial skeleton of the robust australopithecines would have resulted in a loss of structural support to the posterior part of the upper jaw, thus increasing the magnitude of dorsoventral shear stress within the midpalatal suture. Thickening of the anterior hard palate, having the effect of increasing the area of this suture, was said to be an adaptation that compensated for its greater instability.

In his discussion of palatal thickening in the robust australopithecines Rak suggested further that the magnitude of the shear stress present in the midpalatal suture should naturally increase as the lateral buttress moves anteriorly because such migration would create a longer lever arm (posterior tooth row) to act upon the site of attachment of the two halves of the dental arcade. In fact, the improvement in leverage established by an anterior placement of the masseter muscle mass would reduce the force required for equivalent bolus compression and thereby also reduce (and not increase) any shear stress generated in the midpalatal suture. For this reason it was concluded that this particular aspect of the model need not be considered further.¹ The "sutural reinforcement" model therefore predicts that, as a direct consequence of increased instability of the midpalatal suture produced by withdrawal of the masseteric buttress anteriorly, the thickness of the anterior hard palate will be positively correlated with the length of the palate posterior to the masseteric buttress.

¹It was also suggested by Rak that the considerable height of the anteriorly deep palate characteristic of some *P. boisei* specimens (i.e., OH 5 and KNM-ER 405) functions to oppose shear strain in the midpalatal suture and thereby structurally replaces palatal thickening in these specimens. Given that shear stress occurs within the plane of reference (i.e., the midpalatal suture), simply altering the shape of said plane will not affect its magnitude. There is therefore no mechanical basis for the above claim.

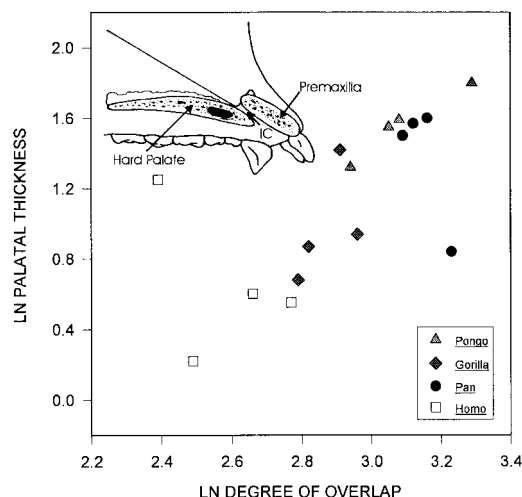


Fig. 2. A plot of degree of overlap of subnasal elements vs. palatal thickness in extant large-bodied hominoids. Data points represent single-sex means calculated for young (patent spheno-occipital synchondrosis) and fully mature (fused spheno-occipital synchondrosis) adults (See Table 1). IC = incisive canal.

Subnasal morphology

The subnasal morphology of large-bodied hominoids differs from that of all other primates in that the premaxilla overlaps the hard palate in the subnasal region (Fig. 2). As is discussed more fully by McCollum and Ward (1997) an overlap of elements along the nasal cavity floor is significant in that the palatal nasal lamina, usually separated from the premaxillary nasal lamina by the palatine fenestra and therefore a relatively independent component of the nasal floor in other primates, is in hominoids structurally "linked" with the premaxillary nasal lamina during ontogeny. This linkage of subnasal elements occurs by virtue of the respiratory mucosa, a pseudostratified columnar ciliated epithelium overlying a highly vascularized and glandular lamina propria, that lines the nasal cavity floor (Cormack, 1993). Throughout facial morphogenesis, a process characterized by extensive growth and displacement of the midfacial skeleton, the overall enlargement and normal functioning of the respiratory mucosa regulates the remodeling activities of the osteogenic tissues (i.e., periosteum; see Enlow, 1990) to maintain requisite spatial relations of the nasal capsule with the remainder of the facial

skeleton. As has been documented in longitudinal studies of human midfacial growth and remodeling (Björk and Skieller, 1972, 1976), one of the key relationships that is maintained throughout the growth process is a stable inclination of the nasal cavity floor with that of the anterior cranial base.

Although a distinguishing feature of large-bodied hominoid crania, the amount of overlap of subnasal elements varies considerably among taxa (Ward and Kimbel, 1983; Begun, 1992, 1994; McCollum et al., 1993; McCollum and Ward, 1997). In extant species, the thickness of the hard palate in dentally mature individuals tends to covary with the extent of overlap of subnasal elements (Fig. 2). In both gorillas and modern humans, thin hard palates are found in association with a minimal degree of overlap of subnasal elements. In comparison, the thicker hard palates of *Pongo* and *Pan* are associated with substantially greater overlap measures. In *Paranthropus*, thick hard palates occur in association with overlap measures that are comparable to or somewhat greater than those observed in *Pongo* and *Pan* (McCollum et al., 1993). This pattern of covariation suggests that the extent to which the premaxilla overlaps the palatine process of the maxilla may be a contributing factor mediating the thickness of the hard palate in these taxa. The "subnasal morphology" model therefore predicts that the thickness of the hard palate is positively correlated with the degree of overlap of subnasal elements.

Posterior facial hyperplasia

The *Paranthropus* masticatory adaptation was one in which powerful muscular bite forces were evenly distributed over a greatly expanded dental occlusal area and one of the morphological correlates of this masticatory adaptation is a vertically tall posterior facial skeleton (Crompton and Hiiemae, 1969; Du Brul, 1974, 1977; Ward and Molnar, 1980; Walker, 1981; Demes and Creel, 1988). The "posterior facial hyperplasia" model proposes that the extreme thickness of the hard palate in *Paranthropus* is simply a structural byproduct of the development of the unusually tall posterior facial skeleton characteristic of these taxa.

That the possession of a disproportionately tall posterior facial skeleton was a significant factor in *Paranthropus* facial ontogeny was first suggested by Bromage (1989), who recognized that the development of this feature would have been associated with an extreme form of *posterior facial hyperplasia*, a growth process in which vertical growth of the posterior maxilla exceeds that which occurs anteriorly (Fig. 3a). Björk and Skieller (1976) have suggested that this particular pattern of midfacial growth, which is said to be characteristic of all anthropoids (Enlow and Azuma, 1975; Bromage, 1992), occurs when the rate of vertical growth of the mandibular ramus (and associated posterior facial skeleton) exceeds that of the nasal airway.

With respect to subnasal morphology, posterior facial hyperplasia is significant in that it results in an upward (or forward) rotation of the anterior maxilla during ontogeny (Fig. 3b; Björk and Skieller, 1976). This rotation of the maxilla relative to the otherwise stable nasal and oral functional capsules (and in particular the soft tissue structures that line these elements, see above) further results in both increased resorptive activity along the anterior nasal cavity floor and increased inferior drift of the oral palatal lamina and anterior dentition (Fig. 3b; Björk and Skieller, 1976; Bromage, 1989; Enlow, 1990). According to Bromage (1989), the extreme upward maxillary rotation assumed to have been characteristic of *Paranthropus* facial ontogeny would have further resulted in the development of a number of features that distinguish these specimens from other taxa. One such feature is the anteriorly shallow palate which was said to result from an increased inferior drift of the anterior hard palate that was itself a product of an increased resorption of the anterior nasal cavity floor.

Bromage did not consider the thickness of the hard palate in his discussion of *Paranthropus* facial form. Rather, his conclusions regarding palatal morphogenesis imply that this element, seemingly composed of a single lamina of compact bone, simply drifted inferiorly during maturation without any significant change in vertical dimension. This is not an entirely accurate characterization of

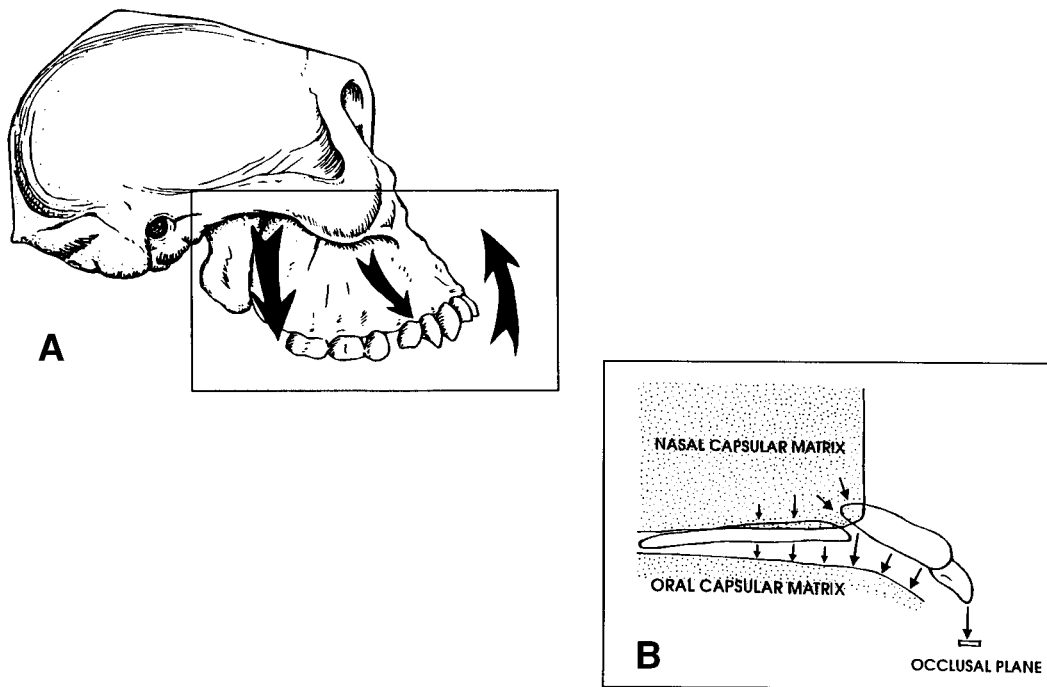


Fig. 3. **A:** Diagram illustrating posterior facial hyperplasia in *Paranthropus*. Increase in the vertical dimension of the posterior maxilla exceeds that anteriorly, resulting in an upward rotation of the anterior face during ontogeny. **B:** Remodeling activities accompanying upward maxillary rotation. Upward maxillary rota-

tion effects increased resorptive activity nasally, increased depositional activity orally and vertical drift of the anterior dentition. Also accompanying this process but not shown is increased resorption along the nasoalveolar clivus.

either palatal morphology or palatal morphogenesis. For example, in humans, the anterior region of the hard palate is typically composed of two cortical laminae separated by an intervening diploic space (Enlow, 1968). During ontogeny the anterior hard palate is continually remodeled through a combined process of periosteal apposition and endosteal resorption on the oral lamina together with endosteal apposition and periosteal resorption on the nasal lamina (Enlow and Bang, 1965). In comparison, the posterior hard palate often comprises only a single lamina of compact bone which is remodeled through the deposition of new bone orally and resorption of bone nasally. Although the full extent of the palatal nasal lamina is resorptive in modern humans, the same is not necessarily true of all primate taxa. In the relatively more prognathic macaque, in which nasomaxillary translation during ontogeny is characterized by a com-

paratively greater anteriorly directed component, only the anterior portions of the nasal cavity floor are consistently resorptive. Posteriorly the nasal laminae of the palatal horizontal shelves are often depository (McNamara et al., 1976; Enlow, 1990). The characteristic pattern of nasal floor remodeling in extant non-human hominoid taxa is currently unknown.

It is therefore apparent from details of palatal morphology in humans that the anterior portions of this element comprise two functionally independent (in terms of facial functional capsules) laminae (Moss and Greenberg, 1967). With respect to palatal morphogenesis, as the extent of inferior drifting of the palatal nasal lamina is regulated primarily by body size and the height of the nasal airway (Kean and Houghton, 1987; Burke and Hughes-Lawson, 1989), whereas depositional activity orally is presumably more a function of the extent of

upward maxillary rotation associated with elongation of the posterior face (Björk and Skieller, 1976), it might be expected that a general thickening of this element might accompany posterior facial hyperplasia. The "posterior facial hyperplasia" model therefore posits that the vertical dimension of the hard palate is structurally linked to that of the posterior facial skeleton. This model predicts a positive correlation between palatal thickness and posterior facial height in hominoid crania.

MATERIALS AND METHODS

Analytical design

The models of palatal thickening described above each propose a link, be it either mechanical or structural in nature, between a specific craniofacial variable and the thickness of the hard palate. Although each model is described independently, this is not to imply that they are considered to be mutually exclusive. Such an assumption is unwarranted given current understanding of the craniofacial growth process and the complex interrelationships that exist among multiple developmental factors (e.g., genetic, mechanical, structural; see Chapter 8 of Enlow, 1990). Rather, the purpose of treating each model independently is to determine whether any one potential developmental factor outweighs the others with respect to the thickness of the hard palate in mature hominoid crania.

In the absence of sufficient experimental data with which to directly evaluate these models, an indirect approach, in the form of correlational analyses, was used to identify associations among craniofacial variables that are consistent with their predictions. In this particular study, an intraspecific ontogenetic approach was preferred over adult interspecific comparisons for several reasons. First, although mechanical and structural relationships among skeletal variables are likely to transcend taxonomic boundaries, these relationships may be difficult to ascertain from interspecific adult samples where extensive taxonomic variation in body size, craniofacial form (e.g., airorhynch vs. klinorhynch) and masticatory adaptation potentially confound results of correlation. The use of ontogenetic data alleviates the

need to control for variables such as these. Instead, intraspecific ontogenetic analyses require only that variation in body size between individuals of the same taxon be "controlled." A second reason to evaluate models of palatal thickening intra- rather than interspecifically concerns the nature of the sample. Although the sutural reinforcement and posterior facial hyperplasia models of palatal thickening apply to anthropoid primates in general, the subnasal morphology model applies only to those species in which an overlap of subnasal elements occurs within the subnasalveolar region. In this regard, the latter model can be evaluated only among the four large-bodied hominoid taxa. The reliability of statistical results obtained from a sample of such small size ($n = 8$ single-sex means) is questionable.

In light of this analytical design it is clear that the elimination of "size" from the variables under investigation is a critical aspect of this study. There are essentially two types of size-adjusted data commonly employed in comparative studies: 1) *residuals* from allometric regression, or 2) *ratios* between variables or shape ratios. Briefly, in the regression-based methods an allometric line, assumed to reflect functional equivalence at different body sizes, is used as a "criterion of subtraction" to remove the effects of body size from the variables of interest (Hartman, 1983, 1988; Reist, 1985; Smith et al., 1986; Harvey and Pagel, 1991; Albrecht et al., 1993). In ontogenetic allometry, regression parameters characterize the progressive increase in the average value of a biological variable with increasing body size (Shea, 1985a; Martin and Barbour, 1989). Residuals calculated from a best-fit line obtained from an ontogenetic sample, while invariably incorporating some measurement error, nevertheless are interpreted to represent components of growth and development beyond those related to simple size increase (Pagel and Harvey, 1989).

Correlations of "size-free" variables obtained from ontogenetic allometry potentially provide strong evidence in support of their developmental association. However, regression methods of size-correction are not without their problems. As has been reviewed extensively by Corruccini (1987,

TABLE 1. Summary of extant hominoid sample

Dental/cranial developmental stage	<i>Pongo</i>			<i>Gorilla</i>			<i>Pan</i>			<i>Homo</i>	
	♂	♀	?	♂	♀	?	♂	♀	?	♂	♀
Deciduous—M ¹ erupting	6	8	2	10	9	9	4	7	19	7	7
M ² erupting	3	5	3	16	11		7	6		3	7
M ³ erupting	6	5		2	7		2	4		13	6
Basilar suture patent	12	6		9	9		7	9		4	5
Basilar suture fused	10	10		11	9		11	11		10	11

1995), regression adjustment is very much sample-labile, tends to discard any sort of shape variation that may be correlated with size and often creates unrealistic similarity between the largest and smallest points along the line. Corruccini (1987, 1995) and others (e.g., Jungers et al., 1995) advocate instead the use of size adjusted variables in the form of ratios in which a geometric mean, one of the members of the Mosimann family of size variables, serves as a measure of overall size. In the present analysis both residual- and ratio-based data were used to evaluate models of palatal thickness in *Paranthropus*.

Sample

Taxonomic samples represent mixed-sex, ontogenetic series of *Pongo pygmaeus* (n = 71), *Gorilla gorilla* (n = 93), *Pan troglodytes* (n = 68) and *Homo sapiens* (n = 72). The African ape and human samples are housed in the Hamann-Todd Osteological Collection, Laboratory of Physical Anthropology, Cleveland Museum of Natural History. The *Pongo* sample comes from the primate collections of the Department of Mammalogy, National Museum of Natural History, Smithsonian Institution. The composition of these samples in terms of both sex and dental/cranial developmental stage is presented in Table 1.

Although not incorporated into the statistical analyses outlined below, some information regarding early hominid craniofacial development and variation can be discerned through examination of the adult cranium. The fossil metrics included within the present analysis are derived from two sources. Palatal thickness dimensions are taken from McCollum et al. (1993). In that analysis palatal thickness was measured from the original fossil material. The remaining craniofacial variables were measured on casts

of late juvenile or adult African Plio/Pleistocene cranial remains purchased from the Wenner-Gren Foundation or Transvaal Museum or provided by the National Museums of Kenya. As is discussed in McCollum (1994), comparison of standard anthropometric measures obtained from the cast material with those available in the original fossil descriptions or subsequent analyses reveals that the cast measures closely approximate those recorded from the original specimens. As in the former analysis, *Australopithecus afarensis* is not included in the fossil sample due to the incomplete nature of the majority of this taxon's representative specimens currently available for examination.

Craniofacial measurements

The linear dimensions collected in this study (Table 2; Fig. 4) were taken either from tracings of specially prepared lateral radiographs (palatal retraction, degree of overlap) or directly from the dry skull (all remaining variables). Prior to radiography, fine wires were extended through the incisive canal and tightly wrapped around both the hard palate and the premaxilla and lead shot was secured to the masseteric tubercle. The demarcated skeletal structures were traced and measurements were taken from the tracings using slide calipers accurate to 0.1 mm.² All radiographic measures were taken parallel to the occlusal plane and were later corrected for parallax effects. The majority of external measures were recorded to the nearest 0.1 mm using slide calipers and all measurements were taken from the right side of the cranium whenever possible. Palatal thickness was measured with spreading

²For a number of human crania used in this study, sagittal sectioning has damaged the incisive canal, thus preventing reliable wrapping of subnasal elements. In these specimens overlap of subnasal elements was measured by tracing the hard palate and "premaxilla" from full-scale photographs of the sagittally sectioned crania.

TABLE 2. Description of craniofacial variables

Palatal thickness	Vertical thickness of palate immediately posterior to incisive fossa
Sutural reinforcement	
Palatal retraction ¹	Horizontal chord distance between masseteric tubercle and posterior nasal spine
Subnasal morphology	
Degree of overlap ¹	Horizontal chord distance between the most anterior aspect of the maxillary palatine process and the posterior pole of the premaxilla
Posterior facial hyperplasia	
Posterior facial height ¹	Vertical chord distance between the articular eminence and the occlusal plane
Additional variables	
Basicranial length	Nasion-basion chord distance
Bitympanic breadth	Maximum horizontal distance between most lateral aspects of tympanic plates
Palatal length	Prosthion-posterior nasal spine chord distance

¹Measured normal to the occlusal plane.

calipers accurate to 0.5 mm. Posterior facial height was measured normal to the occlusal plane and was recorded to the nearest 1.0 mm using steel tape.

Statistical methods

Intraspecific bivariate correlation analyses were performed independently on data sets comprising the two different size-adjusted variables: residuals and shape ratios. For the residual data set, within each taxon the relevant mechanical and non-mechanical craniofacial variables and palatal thickness were regressed upon the geometric mean of basicranial length, bitympanic breadth, and palatal length. Reduced major axis (RMA) regression was performed on the individual cases of natural log-transformed variables derived from each taxonomic sample. RMA parameters were initially calculated separately for each sex and significance ($P < 0.05$) of sex-specific slopes (b) was determined through calculation of the T-statistic provided by Clarke (1980). In cases where sex-specific RMA slopes were found to be non-significant, significance of sex-specific intercepts was determined

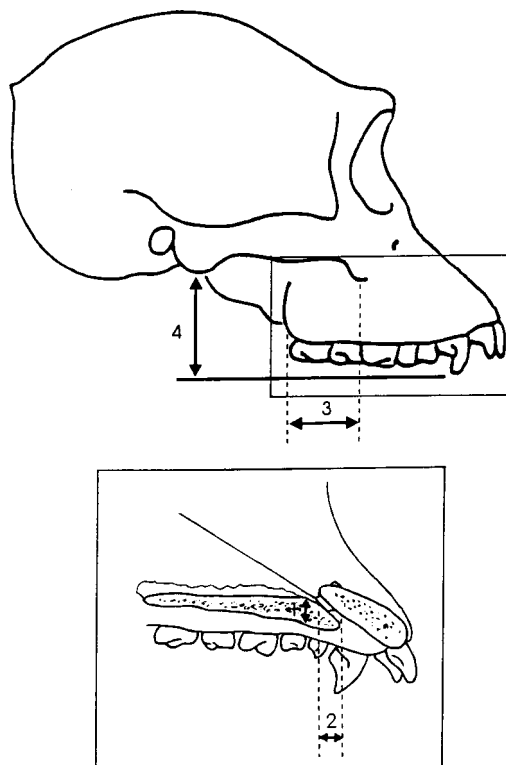


Fig. 4. Diagram illustrating the craniofacial measurements used in this study. 1 = palatal thickness, 2 = degree of overlap, 3 = palatal retraction, 4 = posterior facial height. See Table 2 for further details.

through computation of the z-statistic described by Imbrie (1956). In the absence of significant sexual variation in regression, RMA parameters were recalculated from samples expanded to include subadult individuals of unknown sex. Residuals were calculated only for those variables that scale significantly with measures of cranial/body size during ontogeny and were computed separately for each sex if deemed appropriate. Both Spearman's rank-order correlation coefficient (r_s) and Kendall's coefficient of rank correlation (τ) were used to assess the strength of correlations between relevant size-corrected or log-transformed craniofacial variables and palatal thickness ($P < 0.05$).³

³Palatal thickness measures (both raw and log-transformed) were found to be non-normally distributed in *Pan* (McCollum, 1995).

TABLE 3. RMA regression parameters

× Geometric mean		r^2	y-intercept	Slope	95% CL slope
Palatal thickness	<i>Pongo</i>	0.03ns	—	—	—
	<i>Gorilla</i>	0.08	−16.46	3.75	3.52/4.00
	<i>Pan</i>	0.12	−18.03	4.35	3.78/5.02
	<i>Homo</i>	0.01ns	—	—	—
Palatal retraction	<i>Pongo</i>	0.06ns	—	—	—
	<i>Gorilla</i>	0.48	−5.25	1.81	1.16/2.00
	<i>Pan</i>	0.49	−6.03	2.00	1.82/2.20
	<i>Homo</i>	0.21	−8.24	2.60	2.27/2.98
Subnasal overlap	<i>Pongo</i>	0.35	−4.89	1.76	1.55/2.02
	<i>Gorilla</i>	0.14	−3.06	1.25	1.11/1.41
	<i>Pan</i>	0.64	−4.04	1.59	1.44/1.75
	<i>Homo</i>	0.01ns	—	—	—
Posterior facial height	<i>Pongo</i>	0.69	−3.12	1.53	1.41/1.66
	<i>Gorilla</i>	0.81	−3.11	1.50	1.1/1.60
	<i>Pan</i>	0.62	−2.79	1.41	1.82/2.20
	<i>Homo</i>	0.25	−4.02	1.70	1.49/1.94

ns, non-significant.

The reduced major axis line-fitting technique was preferred over least-squares (LS) regression due to the former model's ability to provide a better estimate of the functional relationship between variables (Rayner, 1985; Pagel and Harvey, 1988, 1989; Aiello, 1992), which in this case is simply the relationship between craniofacial dimensions and cranial/body size. However, as noted by Pagel and Harvey (1988), the reduced major axis model, unlike least-squares regression, is unable to compute deviation scores (residuals) that are completely independent of the x variable. In order to ensure that partial confounding with x (cranial/body size) is not responsible for any significant correlations observed between RMA-derived residuals, correlation analyses were duplicated on residual data sets derived from least-squares regression. As in the RMA analyses, LS residuals were calculated only for those variables that scale significantly with cranial/body size and were computed separately for each sex if deemed necessary by ANCOVA analyses ($P < 0.05$). Consequently, two data sets were evaluated for each of these comparisons and residual variables were concluded to be associated only when significant correlations of RMA-based residuals were verified by similar correlations of LS-based residuals.

In the second analysis shape ratios were calculated for all included specimens (both known and unknown sex) by dividing each variable by the geometric mean of the three size variables (i.e., basicranial length, bitym-

panic breadth, palatal length). As in the above analyses both Spearman's and Kendall's correlation coefficients were used to assess the strength of correlations between relevant shape ratio variables.

RESULTS

Residual variables

The majority of craniofacial dimensions scale positively with increasing cranial size during ontogeny (Table 3). Notable exceptions to this conclusion include palatal thickness in both *Pongo* and *Homo*, palatal retraction in *Pongo* and the degree of overlap in *Homo*, all of which fail to scale significantly with cranial size during ontogeny. Although statistically significant, the association of facial variables, and in particular palatal thickness, with the geometric mean is not remarkably strong. Values of r typically range between 0.3 and 0.7, and are notably higher only with respect to the height of the posterior facial skeleton. Corresponding r^2 values confirm the fairly loose fit of these data (Table 3). Slope values obtained from RMA procedures indicate moderate to strong positive allometric growth of all craniofacial variables relative to increasing cranial size (Table 3). As is expected given the LS model's assumption regarding error variance, slopes calculated from LS procedures are consistently lower than those derived from the RMA model (results not shown).

Table 4 lists the results of the intraspecific correlation analyses performed on the regres-

TABLE 4. Results of correlations—residuals¹

× Palatal thickness	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
Palatal retraction	0.07ns/0.07ns	0.38**/−0.02ns	0.18ns/0.04ns	0.12ns/0.05ns
Subnasal overlap	0.13ns/−0.02ns	0.39**/0.17ns	0.07ns/−0.10ns	−0.20ns/−0.20ns
Posterior facial height	0.26ns/0.18ns	0.04ns/−0.06ns	0.38***/0.25*	−0.01ns/−0.14ns

¹ Spearman correlation coefficients computed for RMA/LS-derived residuals (values of Kendall's τ do not differ from presented results).

ns, non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 5. Correlations of shape ratio values with the geometric mean¹

× Geometric mean	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
Palatal thickness	−0.25 ²	−0.04ns	0.14ns	−0.08 ²
Palatal retraction	−0.29 ²	0.14ns	0.36**	0.09ns
Subnasal overlap	0.02ns	−0.30**	0.28*	−0.33 ²
Posterior facial height	−0.24*	0.45***	0.20ns	−0.02ns

¹ Spearman's r .

² Original variable is uncorrelated with the geometric mean; therefore correlation is spurious (see Jungers et al., 1995).

ns, non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 6. Results of correlations—shape ratios¹

× Palatal thickness	<i>Pongo</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Homo</i>
Palatal retraction	−0.08ns/−0.05ns	−0.03ns/−0.02ns	0.10ns/0.07ns	−0.06ns/−0.04ns
Subnasal overlap	0.04ns/0.03ns	0.15ns/0.10ns	−0.05ns/−0.03ns	−0.13ns/−0.09ns
Posterior facial height	−0.22ns/−0.15ns	−0.09ns/−0.07ns	0.28**/0.19**	0.12ns/0.018ns

¹ Spearman/Kendall correlation coefficients.

ns, non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

sion-adjusted data sets. Statistically significant correlations between variables were identified only within the African ape samples. In the RMA-based analysis, residual values of palatal thickness correlated positively with similar values of palatal retraction and subnasal overlap in *Gorilla*. However, in neither case were these correlations confirmed in the LS-based analysis (Table 4). In *Pan*, residual values of palatal thickness correlate positively, albeit weakly, with similar values of the height of the posterior facial skeleton. This single significant correlation was confirmed in the LS-based analyses. None of the remaining correlations were found to be statistically significant.

Ratio-adjusted variables

Table 5 provides results of intraspecific correlations of ratio-adjusted raw variables with the geometric mean. For those original variables that correlate positively with size (i.e., for all variables except palatal thickness in *Pongo* and *Homo*, palatal retraction in *Pongo* and subnasal overlap in *Homo*; see

Table 3), the results presented in Table 4 give an indication of the magnitude of the association between size and the ratio value (Mosimann and James, 1979; Falsetti et al., 1993; Jungers et al., 1995). From these results it is apparent that some residual size is retained within the variables of posterior facial height in both *Pongo* and *Gorilla*, and palatal retraction and subnasal overlap in *Pan*. However, given that size has been eliminated from all palatal thickness values, the residual size retained within these variables is not of major concern.

Table 6 lists the results of intraspecific correlations analyses performed on the shape ratio data. The results of correlations using shape ratios confirm those obtained from the residual data sets (Table 4). Of the various facial variables considered, the thickness of the palate correlates only with the height of the posterior facial skeleton. Among extant great apes and modern humans this correlation of facial variables appears to be unique to chimpanzees.

DISCUSSION

Mechanical considerations

Evaluations of mechanical models of the upper jaw, such as that provided by Rak (1983), are frustrated by the general absence of experimentally derived information concerning the loading environment of the midpalatal suture during mastication. However, results of the present study offer little support to the proposition that the vertical thickness of the hard palate is an increasing function of stress magnitudes presumed to be associated with the distance separating the posterior palate from the masseteric buttress. These results are perhaps not all that surprising. Rak's model implies that the response of the midpalatal suture to elevated stress levels is necessarily one of palatal thickening. However, several experimental analyses have demonstrated a correlation between the magnitude of extrinsic forces applied to sutures and the extent of their *interdigitation* (e.g., Moss, 1961; Isotupa et al., 1965; Foley and Kokich, 1980; Katsaros et al., 1994). The mechanical role of sutural interdigitations is thought to reside in their ability to effectively transmit force from one bone to another either through bony surfaces directly and/or by means of connective tissue fibers joining the sutural interfaces (Herring, 1972; Wagemans et al., 1988). The increase in cross-sectional area afforded by interdigitations reduces the force per unit area (stress) to which the bony surfaces are subject while simultaneously increasing the area of useful fiber attachment. In light of these considerations, if it is indeed true that the level of stress within the midpalatal suture of *Paranthropus* was high (due either to jaw architecture or dietary specialization), then it might be expected that the response of this structure would have been one of increased sutural interdigitation rather than palatal thickening, a conclusion that seems more probable given the high energetic cost of building up and maintaining unusually thick cortical bone (Bouvier and Hylander, 1981).

It could conceivably be argued that shear magnitudes in the *Paranthropus* palate were so great as to warrant a further increase in

sutural cross-sectional area that could only be achieved through palatal thickening. However, even this does not appear to be a common or perhaps even reasonable solution upon the part of sutures to resist high masticatory stress. Herring (1972), in a functional analysis of cranial suture morphology in pigs (*Suidae*) and peccaries (*Tayassuidae*), suggested that butt-ended sutures, such as the midpalatal suture, resist unusually high levels of stress, and in particular shear stress, by premature fusion. This conclusion derived from her finding that fusion of the palatal sutures in peccaries, whose relatively greater reliance on the upper anterior dentition in foraging activities is presumably associated with increased levels of palatal stress, occurs much earlier than it does in pigs, which do not use their anterior dentition in a similar manner. Although the exact causes of sutural fusion have yet to be firmly established (Herring, 1993), additional evidence in support of the relationship between differential stress and premature synostosis comes from studies of mandibular mechanics which indicate that the partial and complete fusion of the mandibular symphysis typical of some prosimian primates ultimately reflects high levels of dorsoventral shear stress within this structure (Beecher, 1977, 1979, 1983; Ravosa and Hylander, 1994; Ravosa and Simons, 1994).

From the above discussion it is apparent that the mechanical model of palatal thickening in *Paranthropus* provided by Rak is not entirely consistent with current knowledge of sutural mechanics. However, alternative mechanical models of palatal thickening are not immediately apparent. It is generally believed that the upper jaw, unlike the mandible, does not experience a cyclic pattern of continuous deformation during the opening, closing and power strokes of mastication (Hylander, 1977, 1979a,b, 1984, 1985; Hylander et al., 1987; Hylander and Johnson, 1994). Rather, it is more likely that the upper jaw functions primarily as a site of absorption for bite reaction forces generated during the power stroke (Russell and Thomason, 1993). Attempts have been made to correlate the morphology of the upper jaw with patterns of shear, bending and torsion

thought to occur during the power stroke (Preuschoft et al., 1985, 1986; Preuschoft, 1989; Thomason and Russell, 1986; Russell and Thomason, 1993); however, the results of these analyses have not been particularly satisfying. Russell and Thomason (1993) have concluded from their own analyses of palatal morphology in primitive mammals that other constraints on rostral form (e.g., spatial or structural constraints) override general mechanical factors.

Structural considerations

Of the two non-mechanical explanations of palatal thickening considered, only the posterior facial hyperplasia model is supported by results of this study. The observed positive correlations between both residual values of palatal thickness and shape ratios in *Pan* are consistent with the predictions of the posterior facial hyperplasia model. Definitive explanations for the absence of a significant correlation between palatal thickness and the height of the posterior facial skeleton in the remaining taxa are currently unavailable, but it is certainly possible, if not probable, that the ontogenetic processes underlying the airorhynch skull form typical of *Pongo* differ from those typical of the remaining, more klinorhynch hominoid taxa (Shea, 1985b, 1988; Brown and Ward, 1988; Ross and Henneberg, 1995; McCollum and Ward, 1997). With respect to *Gorilla*, Shea (1983) noted that in comparison to the condition observed in chimpanzees, the nasal capsule of gorillas tends to be located more inferiorly within the facial skeleton. Perhaps it is this fundamental difference in facial architecture that underlies the failure for the vertical thickness of the hard palate to correlate significantly with the height of the posterior facial skeleton in the latter taxon. Regardless, that palatal thickness and posterior facial height are correlated only in chimpanzees indicates that conclusions regarding *Paranthropus* morphogenesis based solely upon these results are provisional at best.

That the pattern of palatal morphogenesis in *Paranthropus*, and in fact all australopithecines, was indeed similar to that observed in the chimpanzee is suggested by

the palatal morphology characteristic of these taxa. Among extant hominoid taxa, chimpanzees are unusual in that palatal thickness values increase during ontogeny (Table 3). As has recently been documented by McCollum and Ward (1997) palatal thickening during chimpanzee craniofacial ontogeny is quite substantial and represents the most significant dimensional change that occurs during subnasal morphogenesis. As has been noted previously, one of the characteristic features of the chimpanzee hard palate is the presence within this element of a *recessus palatinus*, or medial extension of the maxillary air sinus (Cave and Haines, 1940; Tobias, 1967; Ward and Kimbel, 1983; Koppe and Schumacher, 1992). As is revealed by computed tomography (Fig. 5), invasive pneumatization of the chimpanzee hard palate occurs during ontogeny as its nasal and oral laminae become increasingly more separated from one another, i.e., as the hard palate thickens. Although growth data for the fossil taxa are limited, both the young adult *Paranthropus* OH 5 cranium (Tobias, 1967) and the juvenile *Australopithecus* specimen from Taung (Conroy and Vannier, 1987) have been described as displaying a *recessus palatinus*. The presence of a *recessus palatinus* in australopithecine specimens of varying age provide strong evidence in support of the conclusion that, like chimpanzees, palatal thickening characterized australopithecine craniofacial ontogeny. From the results of the present study it is apparent that the vertical dimension of the chimpanzee hard palate is at least partially determined by the height of the posterior facial skeleton. It is of interest, therefore, that palatal thickness values observed for *Paranthropus* are not unlike those expected for chimpanzees with posterior facial height dimensions "grown up" to robust australopithecine size (Fig. 6).

Although several lines of evidence support or are at least consistent with the hypothesis that the thickened hard palate of *Paranthropus* developed as a simple structural response to vertical elongation of the posterior facial skeleton, some *A. africanus* specimens, in particular the Sts 5 cranium, display posterior facial dimensions similar to

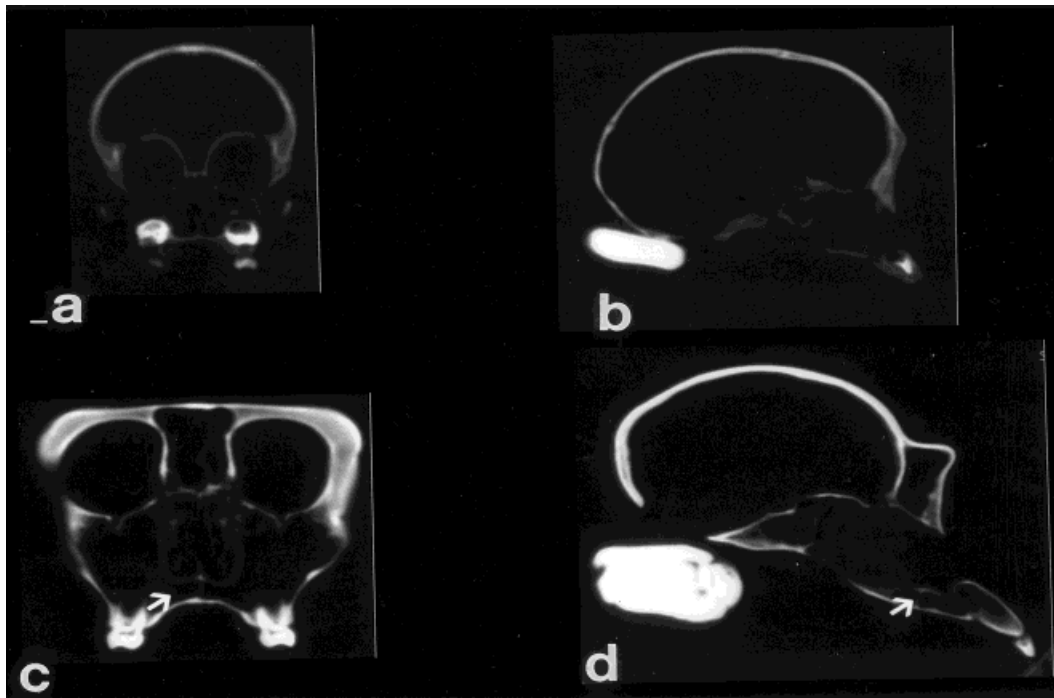


Fig. 5. CT images of the chimpanzee cranium. Anteroposterior (a) and lateral (b) views of an infant of dental/cranial developmental stage 1. Note that the infant palate consists of a single lamina of cortical bone. Anteroposterior (c) and lateral (d) views of a fully adult individual (dental/cranial developmental stage 6). Arrows indicate the *recessus palatinus* of the maxillary air sinus.

those typical of the robust taxa, but do so in the absence of correspondingly thick hard palates (Fig. 6). The failure for specimens such as this to display unusually thickened hard palates suggests that some other factor was involved that either promoted or deterred extreme palatal thickening in australopithecine taxa. The evidence provided by craniofacial biology and comparative australopithecine anatomy suggests the following developmental scenario to account for the variation in palatal thickness observed among these taxa.

During ontogeny, the remodeling of the palatal nasal lamina that accompanies maxillary rotation is presumably mediated only by the spatial demands of the nasal cavity (Fig. 3a). In comparison, the premaxillary contribution to the nasal cavity floor must not only conform to the requirements of the nasal cavity, but also to those of the permanent incisors developing within. With ex-

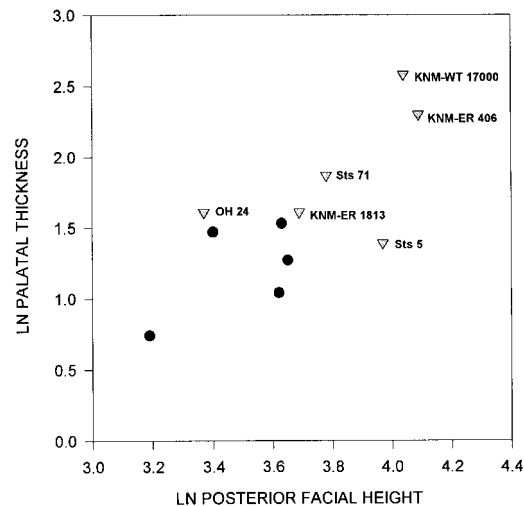


Fig. 6. A plot of the ontogenetic trajectory of palatal thickness vs. posterior facial height in chimpanzees and for all hominids for which these data are available. Data points represent means calculated for each of the age classes defined in Table 1.

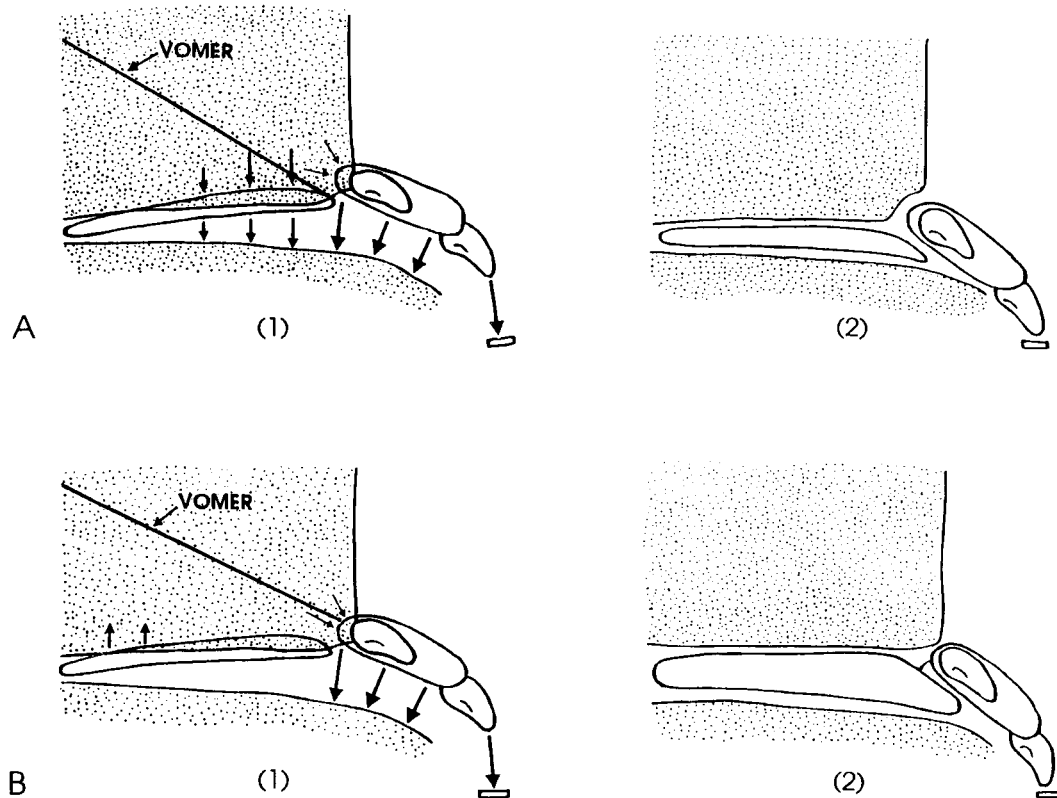


Fig. 7. **A:** Diagram illustrating (1) remodeling of the nasal cavity floor in *A. africanus* and (2) the net result of these remodelling activities. **B:** Diagram illustrating (1) remodelling of the nasal cavity floor in *Paranthropus* and (2) the net result of these remodelling activities. See text for additional discussion.

treme maxillary rotation, such as that believed to have occurred in both *A. africanus* and *Paranthropus*, the amount of resorption required along the premaxillary nasal lamina likely exceeded this element's remodeling capacity. In *A. africanus* the vomer maintains an exclusive attachment to the palatal nasal lamina where it extends below the premaxilla and into the incisive canal (Fig. 1b; Robinson, 1954; Ward and Kimbel, 1983; McCollum et al., 1993). By virtue of this morphology, resorption of the palatal nasal lamina could have continued beyond that of the premaxilla and would have resulted in both a truncated posterior pole of the premaxilla as the nasal cavity expanded around the incisor roots, as well as a markedly "stepped" transition between the premaxilla and hard palate along the nasal cavity floor (Fig. 7a). Significantly, a comparatively short premaxillary component to the

nasal cavity floor is a feature that distinguishes *A. africanus* from other australopithecine taxa (White et al., 1981). Furthermore, although both *A. afarensis* and *A. africanus* have been described as possessing "stepped" nasal cavity floors (Ward and Kimbel, 1983; McCollum et al., 1993), the extent of topographic relief along the nasal cavity floor is indeed relatively greater in the latter taxon (pers. obs).

In comparison to the condition observed in *A. africanus*, the *Paranthropus* vomer extends onto the superior surface of the premaxilla where it inserts immediately behind the attachment site of the cartilaginous nasal septum (Fig. 1c,d; Robinson, 1954; Clarke, 1977; Ward and Kimbel, 1983; McCollum et al., 1993). As the osseous septum essentially defines the transverse plane of the nasal cavity floor, its extension onto the premaxilla precludes any vertical separa-

tion of nasal floor components and indeed *Paranthropus* crania are distinguished from other australopithecine taxa by their possession of a remarkably smooth nasal cavity entrance. The vomeral insertion of *Paranthropus* is developmentally significant in that once rotational movements reached the premaxillary nasal lamina's ability to respond accordingly, further adjustments of the transverse plane of the nasal cavity floor could only have been achieved through increased *depositional* activity posteriorly (Fig. 7b). Depositional activity along the palatal nasal lamina, in combination with continued inferior drift of the palatal oral lamina, would have resulted in an extreme thickening of this element during ontogeny. It should be noted from this scenario of palatal thickening in *Paranthropus* that such a response on the part of palatal remodeling activities to maxillary rotation is very much dependent upon the overlap of subnasal elements along the nasal cavity floor. Therefore, an overlap of subnasal elements, while not a primary determinant of palatal thickness values, is nevertheless an important factor in the process that mediates these values.

Variation in the attachment site of the osseous nasal septum thus provides a reasonable explanation for the variation in palatal thickness observed between *A. africanus* and *Paranthropus*, both of which display a vertically elongated posterior facial skeleton. The non-thickened hard palate of *A. africanus* is presumably associated with this taxon's retention of the primitive great ape septal morphology, which provides for some developmental independence of subnasal components along the nasal cavity floor. In comparison, the greatly thickened hard palate of the robust australopithecines is likely a function of their possession of a derived vomeral insertion that constrained the palatal nasal lamina to conform concurrently to the spatial demands of both the nasal cavity and anterior dentition. Among hominoids this latter morphology is observed only in humans where it is likely a function of the disproportionately small size of the anterior dentition and premaxillary skeletal element. Like humans, *Paranthropus* is also characterized by a disproportionately small anterior dentition (Robinson and

Steudel, 1973; Wood and Stack, 1980) and specimens recovered recently from Swartkrans Member 2 demonstrate the diminutive size of the premaxilla (Clarke, 1988; Grine, 1989). In this respect the vomeral insertion of *Paranthropus* should be considered a derived feature of this taxon that is related to the small size of its anterior dentition and is therefore convergent upon the condition observed in modern humans.

CONCLUSIONS

The present study evaluated three alternative models of palatal thickening in *Paranthropus*. Results of intraspecific bivariate correlation analyses of both residual and shape ratio data sets suggest that the unusually thickened hard palate of *Paranthropus* is best considered a byproduct of the development of an unusually tall posterior facial skeleton. As originally suggested by Bromage (1989) and elaborated upon here, the development of an unusually tall posterior facial skeleton in australopithecine taxa would have been associated with an extreme upward rotation of the anterior maxilla and increased resorptive remodeling activity along the anterior nasal cavity floor. However, by virtue of their possession of a derived nasal septum morphology similar to that observed in humans in which the vomeral insertion occurs on the nasal lamina of the premaxilla, it is proposed that the palatal nasal lamina of *Paranthropus* was constrained by the osseous nasal septum to maintain the approximate level of the premaxillary nasal lamina throughout ontogeny. Adjustments in the transverse plane of the nasal cavity floor in response to maxillary rotation were therefore achieved in this taxon through increased depositional activity posteriorly, rather than increased resorptive remodeling activity anteriorly. The extreme vertical dimension of the hard palate characteristic of adult crania therefore resulted from depositional activity along the palatal nasal lamina during ontogeny. Further direct evaluation of this model of palatal thickening in *Paranthropus*, specifically through an examination of the pattern of nasal floor remodeling as revealed by scanning electron microscopy of bone surfaces, is currently underway.

ACKNOWLEDGMENTS

I thank Bruce Latimer (Cleveland Museum of Natural History) and Richard Thorington (National Museum of Natural History) for access to the extant hominoid collections in their care. I am also grateful for the assistance provided by Lyman Jelima (CMNH) and both Linda Gordon and Jeremy Jacobs (USNMNH) during my numerous visits to their respective institutions. Unlimited access to X-ray facilities was kindly furnished by Linnea Ray and the staff of the Kent State University Health Center. Computed tomography was provided by Eric Blum and his staff at Akron City Hospital. An RMA statistical package was provided by Tim Cole and computer graphics assistance was provided by Richard Sherwood. I am especially indebted to Steve Ward, Owen Lovejoy, Richard Meindl, Brian Shea, and Matt Ravosa for their valuable contributions to this project. Thanks guys! Artwork was provided by Derique Esbrook to whom this manuscript is dedicated. This project was supported by grants from both Sigma Xi and the Boise Fund.

LITERATURE CITED

- Aiello LC (1992) Allometry and the analysis of size and shape in human evolution. *J. Hum. Evol.* 22:127–147.
- Albrecht GH, Belvin BR, and Hartman SE (1993) Ratios as a size adjustment in morphometrics. *Am. J. Phys. Anthropol.* 91:441–468.
- Beecher RM (1977) Function and fusion at the mandibular symphysis. *Am. J. Phys. Anthropol.* 47:325–336.
- Beecher RM (1979) Functional significance of the mandibular symphysis. *J. Morphol.* 159:117–130.
- Beecher RM (1983) Evolution of the mandibular symphysis in Notharctinae (Adapidae, Primates). *Int. J. Primatol.* 4:99–112.
- Begun DR (1992) Miocene fossil hominids and the chimp-human clade. *Science* 257:1929–1933.
- Begun DR (1994) Relations among the great apes and humans: New interpretations based on the fossil great ape *Dryopithecus*. *Yrbk. Phys. Anthropol.* 37:11–63.
- Björk A and Skieller V (1972) Facial development and tooth eruption. An implant study at the age of puberty. *Am. J. Orthodont.* 55:339–383.
- Björk A and Skieller V (1976) Postnatal growth and development of the maxillary complex. In JA McNamara Jr (ed.): *Factors Affecting the Growth of the Midface*. Monograph 6, Craniofacial Growth Series, Ann Arbor: University of Michigan, pp. 61–99.
- Bouvier M and Hylander WL (1981) Effect of bone strain on cortical bone structure in macaques (*Macaca mulatta*). *J. Morphol.* 167:1–12.
- Bromage TG (1989) Ontogeny of the early hominid face. *J. Hum. Evol.* 18:751–773.
- Bromage TG (1992) The ontogeny of *Pan troglodytes* craniofacial architectural relationships and implications for early hominids. *J. Hum. Evol.* 23:235–251.
- Brown B and Ward SC (1988) Basicranial and facial topography in *Pongo* and *Sivapithecus*. In JH Schwartz (ed.): *Orang-utan Biology*. New York: Oxford University Press, pp. 247–260.
- Burke PH and Hughes-Lawson CA (1989) Developmental changes in facial soft tissues. *Am. J. Phys. Anthropol.* 79:281–288.
- Cave AJE and Haines WB (1940) The paranasal sinuses of the African apes. *J. Anat.* 72:493–523.
- Clarke MRB (1980) The reduced major axis of a bivariate sample. *Biometrika* 67:441–446.
- Clarke RJ (1977) The cranium of the Swartkrans hominid SK 847 and its relevance to human origins. Ph.D. dissertation, University of the Witwatersrand.
- Clarke RJ (1988) A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. In FE Grine (ed.): *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, pp. 285–292.
- Conroy GC and Vannier MW (1987) Dental development of the Taung skull from computerized tomography. *Nature* 329:625–627.
- Cormack DH (1993) *Essential Histology*. Philadelphia: J.B. Lippincott.
- Corruccini RS (1987) Shape in morphometrics: Comparative analyses. *Am. J. Phys. Anthropol.* 73:289–303.
- Corruccini RS (1995) Of ratios and rationality. *Am. J. Phys. Anthropol.* 96:189–191.
- Crompton AW and Hiemae KM (1969) How mammalian molar teeth work. *Discovery* 5:23–24.
- Demes B and Creel N (1988) Bite force, diet, and cranial morphology of fossil hominids. *J. Hum. Evol.* 17:657–670.
- Du Brul EL (1974) Origin and evolution of the oral apparatus. In Y Kawamura (ed.): *Frontiers of Oral Physiology*, vol. 1. Basel: Karger, pp. 1–30.
- Du Brul EL (1977) Early hominid feeding mechanisms. *Am. J. Phys. Anthropol.* 47:305–320.
- Enlow DH (1968) *The Human Face: An Account of the Postnatal Growth and Development of the Craniofacial Skeleton*. New York: Harper and Row.
- Enlow DH (1990) *Facial Growth*, 3rd ed. Philadelphia: Saunders.
- Enlow DH and Azuma M (1975) Functional growth boundaries in the human and mammalian face. *Birth Defects: Original Article Series*, Vol. XI (7):271–230.
- Enlow DH and Bang S (1965) Growth and remodeling of the human maxilla. *Am. J. Orthodont.* 51:446–464.
- Falsetti AB, Jungers WL, and Cole TM III (1993) Morphometrics of the callitrichid forelimb: A case study in size and shape. *Int. J. Primatol.* 14:551–572.
- Foley WJ and Kokich VG (1980) The effects of mechanical immobilization on sutural development in the growing rabbit. *J. Neurosurg.* 53:794–801.
- Grine FE (1989) New hominid fossils from the Swartkrans Formation (1979–1986 excavations): craniodental specimens. *Am. J. Phys. Anthropol.* 79:409–449.
- Hartman SE (1983) A critique of some regression adjustments used in allometric size "correction" in numerical taxonomy. *Am. J. Phys. Anthropol.* 62:305–309.
- Hartman SE (1988) Evaluation of some alternative procedures used in numerical systematics. *Syst. Zool.* 37:1–18.
- Harvey PH and Pagel MD (1991) *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Herring SW (1972) Sutures: A tool in functional cranial analysis. *Acta Anat.* 83:222–247.
- Herring SW (1993) Epigenetic and functional influences on skull growth. In J Hanken and BK Hall (eds.): *The*

- Skull, vol. 1: Development. Chicago: University of Chicago Press, pp. 153–206.
- Hylander WL (1977) In vivo bone strain in the mandible of *Galago crassicaudatus*. *Am. J. Phys. Anthropol.* 46:309–326.
- Hylander WL (1979a) Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: An in vivo approach to stress analysis of the mandible. *J. Morphol.* 159:253–296.
- Hylander WL (1979b) Functional significance of primate mandibular form. *J. Morphol.* 160:223–240.
- Hylander WL (1984) Stress and strain in the mandibular symphysis of primates: A test of competing hypotheses. *Am. J. Phys. Anthropol.* 64:1–46.
- Hylander WL (1985) Mandibular function and biomechanical stress and scaling. *Am. Zool.* 25:315–330.
- Hylander WL and Johnson KR (1994) Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *Am. J. Phys. Anthropol.* 94:523–548.
- Hylander WL, Johnson KR, and Crompton AW (1987) Loading patterns and jaw movements during mastication in *Macaca fascicularis*: A bone-strain, electromyographic and cineradiographic analysis. *Am. J. Phys. Anthropol.* 72:287–314.
- Imbrie J (1956) Biometrical methods in the study of invertebrate fossils. *Bull. Am. Mus. Nat. Hist.* 108:215–252.
- Isotupa K, Koski K, and Makinen L (1965) Changing architecture of growing cranial bones at sutures as revealed by vital staining with alizarin red S in the rabbit. *Am. J. Phys. Anthropol.* 23:19–23.
- Jungers WL, Falsetti AB, and Wall CE (1995) Shape, relative size, and size-adjustments in morphometrics. *Yrbk. Phys. Anthropol.* 38:137–162.
- Katsaros C, Kiliaridis S, and Berg R (1994) Functional influence on sutural growth. A morphometric study in the anterior facial skeleton of the growing rat. *Eur. J. Orthodont.* 16:353–360.
- Kean MR and Houghton P (1987) The role of function in the development of human craniofacial form—a perspective. *Anat. Rec.* 218:107–110.
- Koppe T and Schumacher K (1992) Untersuchungen zum pneumatizationsgrad des viscerocranium beim menschen und bei den pongiden. *Acta Anat. Nippon* 67:725–734.
- Martin RD and Barbour AD (1989) Aspects of line-fitting in bivariate allometric analysis. *Folia Primatol.* 53: 65–81.
- McCollum MA (1994) Mechanical and spatial determinants of *Paranthropus* facial form. *Am. J. Phys. Anthropol.* 93:259–273.
- McCollum MA (1995) Palatal Thickening and Facial Form in *Paranthropus*: Evaluation of Alternative Developmental Models. Unpublished dissertation, Department of Anthropology, Kent State University.
- McCollum MA and Ward SC (1997) Subnasalveolar anatomy and hominoid phylogeny: Evidence from comparative ontogeny. *Am. J. Phys. Anthropol.* 102: 377–406.
- McCollum MA, Grine FE, Ward SC, and Kimbel WH (1993) Subnasal morphological variation in extant hominoids and fossil hominids. *J. Hum. Evol.* 24:87–111.
- McNamara JA, Riolo ML, and Enlow DH (1976) Growth of the maxillary complex in the rhesus monkey. *Am. J. Phys. Anthropol.* 44:15–26.
- Moss ML (1961) Extrinsic determination of sutural area morphology in the rat calvaria. *Acta Anat.* 44:263–271.
- Moss JL and Greenberg SN (1967) Functional cranial analysis of the human maxillary bone: I. Basal bone. *Angle Orthodont.* 37:151–164.
- Mosimann JE and James FC (1979) New statistical methods for allometry with applications to Florida red-winged blackbirds. *Evolution* 33:444–459.
- Pagel MD and Harvey PH (1988) Recent developments in the analysis of comparative data. *Q. Rev. Biol.* 63:413–440.
- Pagel MD and Harvey PH (1989) Taxonomic differences in the scaling of brain on body weight among mammals. *Science* 244:1589–1593.
- Preuschoft H (1989) Biomechanical approach to the evolution of the facial skeleton of hominoid primates. *Fortschritte der Zoologie* 35:421–431.
- Preuschoft H, Demes B, Meier M, and Bar HF (1985) Die biomechanischen prinzipien im oberkiefer von langschmahnuzigen wirbeltieren. *Z. Morphol. Anthropol.* 76: 1–24.
- Preuschoft H, Demes B, Meier M, and Bar HF (1986) The biomechanical principles realised in the upper jaw of long-snouted primates. In JG Else and PC Lee (eds.): *Primate Evolution*. Cambridge: Cambridge University Press, pp. 249–264.
- Rak Y (1983) *The Australopithecine Face*. New York: Academic.
- Ravosa MJ and Hylander WL (1994) Function and fusion of the mandibular symphysis in primates: stiffness or strength? In JG Fleagle and RF Kay (eds.): *Anthropoid Origins*. New York: Plenum.
- Ravosa MJ and Simons EL (1994) Mandibular growth and function in *Archaeolemur*. *Am. J. Phys. Anthropol.* 95:63–76.
- Rayner JMV (1985) Linear relations in biomechanics: The statistics of scaling functions. *J. Zool. (Lond.)* 206:415–439.
- Reist JD (1985) An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Can. J. Zool.* 63:1429–1439.
- Robinson JT (1953) *Telanthropus* and its phylogenetic significance. *Am. J. Phys. Anthropol.* 11:445–501.
- Robinson JT (1954) The genera and species of the Australopithecinae. *Am. J. Phys. Anthropol.* 12:181–200.
- Robinson JT and Steudel K (1973) Multivariate discriminant analysis of dental data bearing on early hominid affinities. *J. Hum. Evol.* 2:509–527.
- Ross C and Henneberg M (1995) Basicranial flexion, relative brain size and facial kyphosis in *Homo sapiens* and some fossil hominids. *Am. J. Phys. Anthropol.* 98:575–594.
- Russell AP and Thomason JJ (1993) Mechanical analysis of the mammalian head skeleton. In J Hanken and BK Hall (eds.): *The Skull, vol. 3: Functional and Evolutionary Mechanisms*. Chicago: University of Chicago Press, pp. 345–383.
- Shea BT (1983) Size and diet in the evolution of African ape craniodental form. *Folia Primatol.* 40:32–68.
- Shea BT (1985a) Ontogenetic allometry and scaling: A discussion based on the growth and form of the skull in African apes. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum, pp. 175–205.
- Shea BT (1985b) On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. *Am. J. Phys. Anthropol.* 68:329–342.
- Shea BT (1988) Phylogeny and skull form in the hominoid primates. In JH Schwartz (ed.): *Orang-utan Biology*. New York: Oxford University Press, pp. 233–245.
- Smith RJ, German RZ, and Jungers WL (1986) Variability of biological similarity criteria. *J. Theor. Biol.* 118:287–293.
- Thomason JJ and Russell AP (1986) Mechanical factors

- in the evolution of the mammalian secondary palate: A theoretical analysis. *J. Morphol.* 189:199–213.
- Tobias PV (1967) Olduvai Gorge: The cranium of *Australopithecus (Zinjanthropus) boisei*. Cambridge: Cambridge University Press.
- Wagemans PAHM, vand de Velde JP, and Kuijpers-Jagtman AM (1988) Sutures and forces: A review. *Am. J. Orthod. Dentofac. Orthop.* 94:129–141.
- Walker AC (1981) Diet and teeth. Dietary hypotheses and human evolution. *Philos. Trans. R. Soc. Lond. [B]* 292:57–64.
- Ward SC and Kimbel WH (1983) Subnasal alveolar morphology and the systematic position of *Sivapithecus*. *Am. J. Phys. Anthropol.* 61:157–171.
- Ward SC and Molnar S (1980) Experimental stress analysis of topographic diversity in early hominid gnathic morphology. *Am. J. Phys. Anthropol.* 53:383–395.
- White TD, Johanson DC, and Kimbel WH (1981) *Australopithecus africanus*: Its phyletic position reconsidered. *S. Afr. J. Sci.* 77:445–470.
- Wood BA and Stack CG (1980) Does allometry explain the differences between “gracile” and “robust” australopithecines? *Am. J. Phys. Anthropol.* 52:55–62.